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Farm dams facilitate amphibian invasion: Extra-limital range expansion of the painted reed frog in South Africa

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Abstract Driven by the mobility of organisms and novel habitats created by anthropogenic changes of landscape structure and climate, range expansion can modify the functioning of recipient ecosystems by altering ecosystem processes such as intra- and cross-trophic biotic interactions. We explain the spatial and temporal dynamics of the recent range expansion of painted reed frogs (*Hyperolius marmoratus* Rapp) in the Western Cape Province of South Africa. We identify the geographical and temporal origin of expansion, quantify extent of occurrence, internal range structure and habitat characteristics of occupied sites. The painted reed frog was introduced into its novel range during 1997 or early 1998, and is now widespread. Highly variable annual spread rates suggest both diffusion-based and human-mediated jump dispersal as drivers of the range expansion. Spatial structure is evident at the scale of the entire novel range, with two distinct populations separated by at least 100 km of unoccupied terrain. Models show that occupancy is limited by summer aridity, low winter temperatures and the absence of fringing vegetation around water bodies. The range structure and the presence of breeding populations in 26% of water bodies surveyed imply that there are further opportunities for range expansion across the network of artificial water bodies available. We infer that, facilitated by human-mediated jump dispersal and the dense distribution of perennial farm dams, painted reed frogs have colonized the winter rainfall region of south-western South Africa and fit the description of 'urban exploiters'. Unspecialized habitat requirements, rapid spread and high local population sizes further suggest that they could compete with co-occurring endemic frogs and hamper the conservation of these range-restricted amphibians.

Key words: Anura, biological invasion, extent of occurrence, Hyperoliidae, rate of spread, urban exploiter.

INTRODUCTION

Biological invasions are powerful natural experiments that present ecologists with opportunities to investigate range dynamics in novel environments (Brown & Sax 2004). These dynamics can be understood by quantifying range structure and identifying the factors that contribute to distribution limits (Thomas *et al.* 2004). As the chronologies of range expansion of invasive species are often recorded, the reconstruction of invasion histories improves our understanding of the process of biological invasion. In particular, it is important to be able to identify the causes of range expansion (Didham *et al.* 2005; Parmesan 2006), source populations and entry points (Rollins *et al.* 2011; Ruiz *et al.* 2011), generate hypotheses on the mechanisms of spread and build predictive models of invasion impacts (Kulhanek *et al.* 2011). Reconstruction of invasion history is thus a precursor to studies of invasion dynamics and the causes, mechanisms and limits of invasion (Andow *et al.* 1990).

Without data on invasion history, recognition of invasiveness of a species may be delayed, hampering appropriate response and control measures (Le Maitre *et al.* 2004; McGeoch *et al.* 2012). Delayed recognition of invasiveness may also occur when indigenous species undergo rapid range expansion outside their historical extent of occurrence (so-called extra-limital species – Spear & Chown 2009), as they are less likely to be acknowledged as invasive than those that are alien to the geographical area of interest (Guo & Ricklefs 2010). Invasive populations of extra-limital species may, however, have impacts very similar in nature and scale to those of extra-regional invasive species (Spear & Chown 2008).

Although the conservation status of amphibians globally is in serious decline (Sodhi *et al.* 2008), there is a handful of instances of amphibian species expanding their ranges and becoming invasive (e.g. Fouquet & Measey 2006; Ficetola *et al.* 2007; Phillips *et al.* 2007). Although there are currently no alien invasive amphibians in South Africa (Minter *et al.*

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2004; Van Rensburg *et al.* 2011), three local taxa have established extra-limital populations within the country and are expanding their ranges (Measey & Davies 2011). The painted reed frog (*Hyperolius marmoratus* Rapp, Anura: Hyperoliidae) is one such species, with breeding populations having undergone a range expansion of over 500 km in the south-western areas of South Africa early in the last decade (Tolley *et al.* 2008). The congeneric arum lily frog (*Hyperolius horstockii*) occupies a much smaller range and is endemic to the Cape Floral Region of the Western and Eastern Cape Provinces (Braack 2004). Historically, the two species ranges were non-overlapping, except for a small area in the extreme east of the region, but they are now congruent over large parts. Presence of the two species in the same water bodies could result in competition for calling sites during their overlapping breeding seasons. The rapid extra-limital range expansion of the painted reed frog provides an opportunity to investigate the environmental correlates of a recent range expansion across the majority of its spatial and temporal extent (Boone & Krohn 2000; Sagarin *et al.* 2006).

Ectotherm species ranges are tied closely to temperature and hydrological gradients (Buckley & Jetz 2007). In amphibians this is thought to be due to a tight coupling between thermoregulation and water balance, and the 'leaky boundary' between internal and external environments (Feder 1992), which place limits on the mobility and energy balance of these animals. In consequence, temperature and humidity are generally important determinants of occupancy and abundance in these species (Boone & Krohn 2000; Ficetola *et al.* 2007). The ranges of anuran amphibians, in particular, are expected to be limited by local habitat quality such as vegetation cover, because during prolonged breeding seasons they must periodically leave the water body to feed. Thus, they require aquatic and fringing vegetation for cover and foraging opportunities (Wells 1977); fringing vegetation has also been shown to maintain pond–pond and pond–matrix connectivity for dispersal of juvenile amphibians (Joly *et al.* 2001).

Range expansion may occur through long-distance dispersal, diffusion within a local neighbourhood, or by mixed-mode dispersal where both mechanisms operate simultaneously (Shigesada *et al.* 1995). Amphibians accomplish long-distance dispersal naturally, although rarely, via transoceanic voyages (e.g. Measey *et al.* 2007), linear movement along stream corridors (Lowe 2009) and inter-patch dispersal (Smith & Green 2006). Tolley *et al.* (2008) found discordant geographical structure in mitochondrial DNA sequences among breeding populations of painted reed frogs in the novel range, providing clear evidence in support of human-mediated jump dispersal. However, the novel range was not surveyed extensively, and alternative explanations for the current range structure within the novel range are possible. Specifically, establishment and subsequent spread in the novel range may have occurred via (i) human-mediated jump dispersal, for which there is some empirical support (Tolley *et al.* 2008); (ii) natural diffusion-based dispersal; or (iii) mixed-mode dispersal in different parts of the novel range.

Here we identify the geographical and temporal origin of the range expansion from adjacent parts of the historical range, quantify the internal range structure and estimate rate of spread, and identify environmental correlates of occupancy in the novel range using a static model of habitat variables (Guisan & Thuiller 2005). We predict that the range limits in the novel range will be explained by climatic variables such as temperature, precipitation and evaporation, and the seasonality of these. We predict that habitat quality, particularly the density and size of water bodies available as breeding habitat and the presence of fringing, emergent and floating vegetation at water bodies will be important at a local scale (Table 1). Finally, we use information on range structure and estimated rate of spread to infer possible mechanisms of dispersal and distinguish among the three modes of range expansion, that is, natural diffusion across the novel range, expansion entirely by jump dispersal and expansion by mixed-mode dispersal with different expansion modes in different populations.

METHODS

Study species

The painted reed frog is a widespread pond-breeding species occurring in a range of lentic water body types in savanna and coastal forest, including pans, dams, vleis, and slow-flowing stream and river reaches (Bishop 2004). Little is known about the diet, but several West African *Hyperolius* spp. are generalist arthropod predators, consuming a range of items from six major arachnid and hexapod taxa (Luiselli *et al.* 2004). Adult painted reed frogs are desiccation-resistant (Withers *et al.* 1982), are capable of travelling some distance over land and have a tendency to enter buildings and cargo and to be translocated on fresh produce and nursery plants (Bishop 2004).

The historical range of the species in South Africa extended from the coastal and low-lying areas in the north and east of the country to the central escarpment at approximately 1600 m a.s.l. (Bishop 2004). Passmore and Carruthers (1995) described the south-western boundary of the distribution as the Tsitsikamma Forest, a coastal sub-temperate forest belt extending along the south-eastern coast and ending approximately at the eastern boundary of the Western Cape Province, South Africa (Fig. 1).

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Table 1. Spatial and environmental variables used to explain the distribution of the painted reed frog (*Hyperolius marmoratus*) with published support for their relevance and importance

Variable	Expected relationship with occupancy	Reasoning/preferred range of values	References
Altitude (m a.s.l., centred)	Threshold effect	Historical range is below 1600 m; expect lower altitudinal range at higher latitudes	Parmesan and Yohe (2003); Bishop (2004)
Presence/absence of fringing vegetation at water body	Positive relationship	Sheltered roosting sites preferred, although frequently basks in exposed positions	Passmore and Carruthers (1995); Bishop (2004)
Presence/absence of floating and emergent vegetation at water body	Positive relationship	Usually calls from vegetation above the water surface	Passmore and Carruthers (1995); Bishop (2004)
Mean annual precipitation (mm)	Positive relationship	Indigenous to tropics and subtropics where standing water is required for breeding; chorus attendance is dependent on rainfall	Henzi *et al*. (1995); Passmore and Carruthers (1995); Channing (2001); Bishop (2004)
January potential evaporation (mm; A-pan equivalent)	Negative relationship	Indigenous to tropics and subtropics; humid microhabitats; locomotion increases water loss in anurans	Preest and Pough (1989); Passmore and Carruthers (1995); Channing (2001); Bishop (2004)
Heat units between April and September (degree days, base 10°C)	Positive relationship or threshold effect	Threshold number of degree days may be required for dispersal; locomotion increases water loss; highly desiccation-resistant	Preest and Pough (1989); Schmuck and Linsenmair (1997)
Water body size (ha)	Threshold effect	Very small water bodies may not be suitable at several life stages as they may dry up altogether during the summer (in winter rainfall regions)	Laan and Verboom (1990)
Number of water bodies within 750 m radius	Positive/threshold effect	Usually occurs close to water bodies; call audible over a distance of 400–1000 m	Passmore and Carruthers (1995); S.J. Davies, unpubl. data (2012)

Overview of methods

We used spatially and temporally explicit data collected throughout the period of the range expansion to investigate the range dynamics. We began by pinpointing the spatial and temporal origin of the range expansion from historical records and those collected during this study to define the boundary between the historical and novel ranges. Systematic sampling was then used to collect additional presence and absence records inside the novel range. These were used to map the extent of occupancy and internal range structure. A subset of records which had accompanying habitat information was used to identify the environmental correlates of occupancy using a generalized linear model. Annual rate of spread was quantified by identifying the position of the expanding range boundary at the end of each breeding season.

Origin and initiation of range expansion

The geographical and temporal points of introduction into the novel range were identified in relation to the positions and dates of existing records of species occurrence. Point locality data from the South African Frog Atlas Project Database (Minter *et al*. 2004) and the provincial conservation authority CapeNature's Biodiversity Database (Turner 2006) were used to identify the position and date of the first records beyond the recorded historical range boundary at Tsitsikamma National Park headquarters (34°01′18.8″S, 23°53′47.9″E). The Frog Atlas database included records of species presence from all but one quarter degree square in the Western Cape Province, spanning the years from 1905 to 2003 (Minter *et al*. 2004); CapeNature's Biodiversity Database consisted of observations of species presence from targeted monitoring and incidental observations collected from 1997 to 2008.

Occupancy sampling

Determination of sampling extent

To define the sampling extent for the study we applied a simple diffusion-based spread model based on water body availability and colonization extinction processes in

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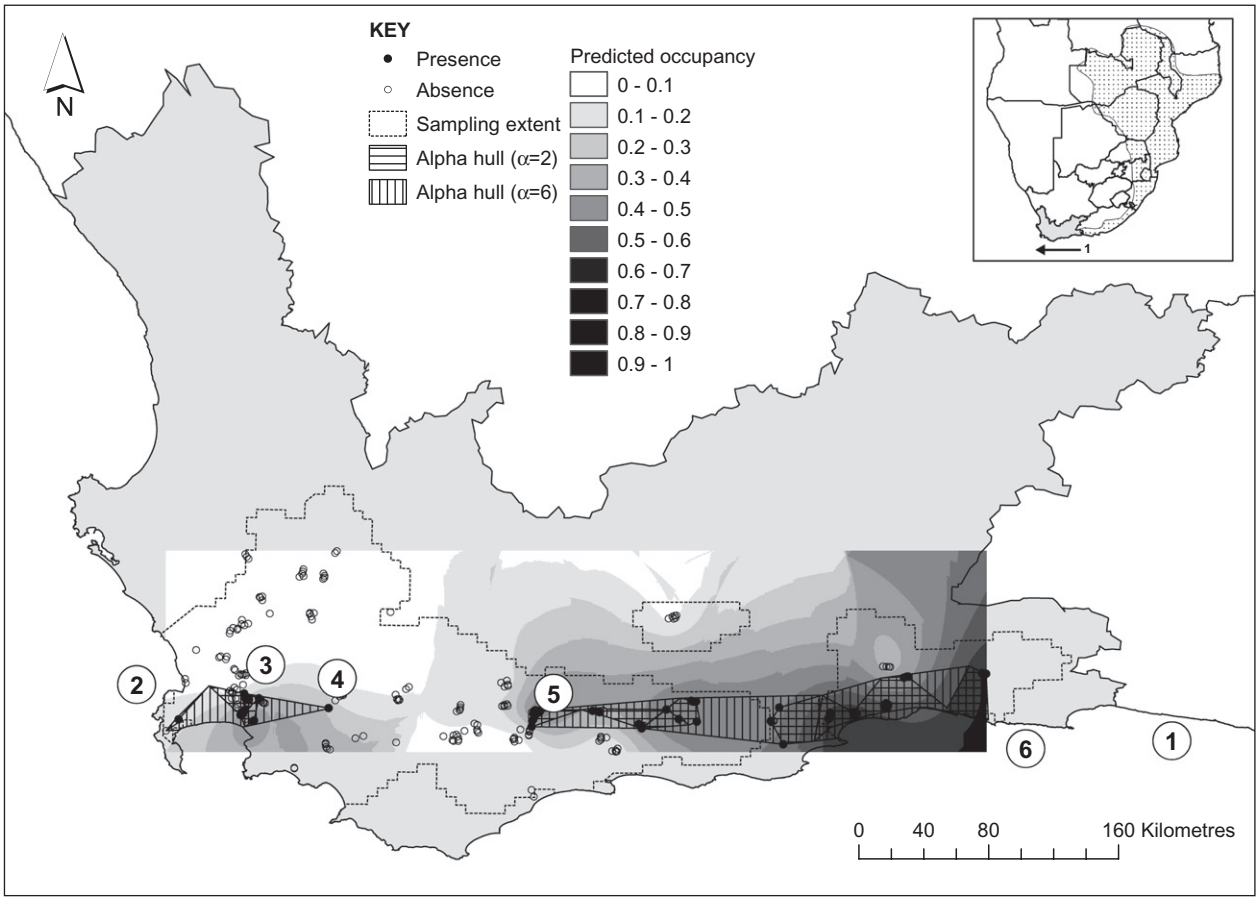

Fig. 1. The novel range of *Hyperolius marmoratus* Rapp in the Western Cape Province, South Africa. Inset shows the historical range (stippled area; redrawn from Channing 2001); arrow shows general direction of range expansion from the putative origin. Localities: 1 – Tsitsikamma National Park headquarters, 2 – Cape Town, 3 – Stellenbosch, 4 – Villiersdorp, 5 – Swellendam, 6 – Knysna. Map projection: geographical; datum: WGS 84. Predicted occupancy is a surface generated from the combined model (ArcMap 9.2 ordinary kriging, spherical semi-variogram model, 1 km fixed radius).

5 km × 5 km grid cells laid over the entire Western Cape Province. In the simulation, frogs were able to move from an occupied cell to one of four neighbouring cells (von Neumann neighbourhood) if $n \geq x + 2$, where n and x were the numbers of water bodies in a neighbouring unoccupied cell and the focal occupied cell, respectively. Colonization and local extinction were modelled stochastically with $col = 1 - e^{-\alpha x}$, where col is the colonization probability per time step, and $\alpha = 0.05$, and $ext = e^{-\beta x}$, where ext is the extinction probability per time step, and $\beta = 0.05$ (see for example Roura-Pascual *et al.* 2009). The modelled range extent at equilibrium (after 440 time steps) was buffered by 10 km to generate the sampling extent. This defined the maximum potential range of the painted reed frog based only on water body availability and colonization extinction processes, and covered 39 804 km^2 (1603 grid cells; Fig. 1).

Detection of breeding populations

Forty grid cells were randomly selected for systematic surveys within the sampling extent. Eight additional cells were visited opportunistically during sampling, giving a total of 48 surveyed grid cells. In each sampled grid cell, two to six water bodies were located by reference to an electronic topographical and water body layer (AfricaTopo Topo GPS maps. http://www.MadMappers.com, 2005) held on a Garmin GPSmap 76CSx global positioning system. Observers visited each water body before dusk to collect habitat data, and returned later the same evening to determine occupancy.

Breeding choruses of painted reed frogs form during the summer breeding season (mid-October to mid-February) and may contain hundreds of males calling from elevated calling sites. The call is a piercing whistle repeated about once per second and is easily audible over 400–1000 m in calm weather (*c.* 104 dB at 50 cm; Passmore 1981). The call is distinct from those of all other frogs in the region. Choruses reach peak intensity approximately 30 min after sunset, after which calling continues until shortly after midnight (Bishop 2004). Occupancy (presence/absence of a breeding chorus) was determined by auditory surveys of advertisement calls at water bodies. Observations were carried out during the peak nocturnal calling period under suitable calling conditions and lasted at least 10 min. Other studies have employed

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similar methods to sample anuran species occupancy (e.g. Olson *et al.* 2012).

Because of the conspicuous nature of the species and its tendency to form large choruses, no misidentification occurred (i.e. no false presences). However, to verify the level of false absence in the sampling, we tested whether the length and number of visits affected the outcome of the presence/absence detection. Five potentially suitable sites that were thought to be unoccupied were visited for an extended duration (20.30 hours to 22.45 hours) on a single night with suitable calling conditions in February 2007. Painted reed frogs were not heard calling at any of the five test sites, although there were active choruses at nearby monitoring sites on all occasions, indicating that visit duration did not affect detection probability. In total, nine sites were visited repeatedly (twice or more; a total of 27 visits). Only one occupied site was omitted as an absence, suggesting a detection rate of 96.3% (=26/27) and a low rate of false absence in the dataset (5.8%; i.e. 11 out of the 196 absences could be presences).

Environmental correlates of occupancy

Occupancy and habitat data were collected between October 2006 and November 2008 for 236 water bodies in the novel range. Ninety-one per cent of the water bodies in the sample were artificial dams, and examination of the topographical data (Chief Directorate Surveys and Mapping 2006) showed a similar high prevalence of artificial water bodies within the sampling extent (88% of mapped water bodies) and the Western Cape Province as a whole (91%). Natural water bodies such as pans, river reaches and seasonally inundated areas were therefore excluded as a category from further analyses of environmental correlates of occupancy because of their infrequent occurrence in the dataset; overall, data for a total of 210 artificial or highly disturbed water bodies were included in the generalized linear model.

Latitude, longitude and altitude of surveyed water bodies were used to perform trend surface analysis (see Appendix S1). The following environmental variables were measured at all sampled water bodies: presence/absence of fringing, floating and emergent vegetation in and around the water body, water body type (dam, river, pan or pond) and water body origin (artificial, natural or disturbed but natural in origin) were estimated visually. Altitude was drawn from the Western Cape digital elevation model (Ver. 1.1, 2002; 300 m resolution; Centre for Geographical Analysis, Centre for Geographical Analysis Stellenbosch University); water body size and density (number of water bodies present within a 750 m radius of each site) were calculated from the electronic topographical and water body layer data using ArcView 3.2a and extensions (Environmental Systems Research Institute, 1992–2000, Redlands, CA, USA; DeLaune 2003; Jenness 2007). Climatic variables (mean annual precipitation, evaporative potential in January and winter degree days) were interpolated $1' \times 1'$ data extracted from the South African Atlas of Agrohydrology and Climatology (Schulze *et al.* 1997).

In total, seven environmental variables, four of which reflect habitat quality and three, climatic conditions, were used to model variation in occupancy; the reasons for including each explanatory variable are given in Table 1 and the descriptive characteristics in Appendix S2. Variables with cross-correlations greater than 0.4 were excluded. The dummy variable describing the presence/absence of emergent vegetation was omitted because of its strong correlation with fringing vegetation (Spearman's *rho* = 0.413). Variables for water body type and origin were excluded as most water bodies in the sample were artificially constructed farm dams (see above).

Modelling approach

A generalized linear model (analysis of covariance with a binary response variable, binomial errors and a logit link function) was used to investigate the relationship between occupancy and the selected explanatory variables. To account for spatial autocorrelation in the occupancy data, the spatial and environmental variables were modelled separately (Legendre & Legendre 1998), and then the minimum adequate spatial and environmental models were concatenated to form a final combined model (hereafter the 'combined model'). The variation explained by the combined model was thus partitioned into (i) non-spatial environmental variation; (ii) spatial structuring shared by the environmental data; (iii) spatial patterns not shared by the environmental data; and (iv) unexplained or residual variation.

We used an *a posteriori*, best-fit approach to model selection (Hobbs & Hilborn 2006). Model simplification was performed using deletion tests with Akaike's Information Criterion (AIC) to assess the effect of removing a given term from the model. Model selection was based on second-order AIC (AIC_c), a measure of relative Kullback–Leibler information content that is suitable for small sample sizes (Anderson & Burnham 2002). All analyses were conducted in R Statistical Software (Ver. 2.8.1; R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria, 2010). The effect of term deletion on goodness-of-fit was assessed using χ^2-tests on nested model pairs (Crawley 2007). In all cases the more parsimonious model was selected, unless the effect of term deletion on goodness-of-fit was significant and AIC_c was reduced by term deletion. To further evaluate model performance, inflation and tolerance were calculated for all main effects in the maximal model, and the maximal and combined models were checked for over-dispersion (Diniz-Filho *et al.* 2003). Spatial autocorrelation analysis was conducted to examine the spatial structure of original data (occupancy) and predicted data from the model, and to test for such structure in model residuals. Moran's *I* statistics were calculated for the final combined model in SAM 4.0 (10 distance classes, equal numbers of point pairs; Rangel *et al.* 2006).

The direction and strength of relationships between the explanatory and response variables in the best-fit model were interpreted in the light of the hypotheses posed. Because we did not intend to use the models for predictive purposes at the scale of individual sites, confusion matrix-derived measures of model performance are not presented.

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Range structure and extent

To calculate the range extent in the novel range we used extent of occurrence and the alpha hull. The alpha hull is a generalization of the convex hull (or minimum convex polygon) that minimizes the influence of outliers, for example, those caused by false absences (Hui *et al.* 2011). Like more complex kernel methods, the alpha hull converges on the true area occupied as the number of data points increases (Getz & Wilmers 2004; Hui *et al.* 2011). Depending on the value of alpha used, the resulting hull can be used to explore internal range structure and identify the position and extent of gaps and patches within the distribution (Burgman & Fox 2003).

Alpha hulls were drawn and measured in ArcView 3.2a and Quantum GIS (Quantum GIS Development Team, Open Source Geospatial Foundation Project, 2010) following the method for threatened species assessments (IUCN Standards and Petitions Subcommittee 2011). Area measurements were made from polygons clipped to the coastline. The alpha values used here (2 and 6) span a range of values used successfully in other studies (e.g. Burgman & Fox 2003; Getz & Wilmers 2004).

Prevalence of painted reed frogs at sampled sites was similar in artificial (26%) and natural water bodies (27%), so records from both types of water bodies were used in the alpha hull analysis; that is, all occupancy records west of the historical range boundary were included ($n = 347$).

Rate of spread

The invasion of the painted reed frog into and across the Western Cape is known to have progressed chiefly from east to west (Minter *et al.* 2004; Tolley *et al.* 2008), rather than in a radial or semicircular pattern as in other invasion processes (e.g. Phillips *et al.* 2007 for cane toads, *Rhinella marina* in Australia). Indeed, the study area as a whole is bounded by mountain ranges in the north and the coastal plain in the south, both of which are likely to constrain latitudinal spread as these mountains impose physical barriers to spread on a north–south axis, and interrupt frontal weather systems that produce most of the Western Cape's winter rainfall and low temperatures (Tyson 1986), producing a steep moisture gradient between the coast and the semi-arid inland regions. Therefore, we focused on (i) the rate of expansion along a linear axis measured as longitudinal distance from the identified point of origin of the range expansion and (ii) increase in total area occupied determined from the area of the alpha hull.

Determinations of rate of spread can be confounded by non-uniform sampling over time and space (Suarez *et al.* 2001). In this study, the majority of sampling effort took place during the Frog Atlas period (1997–2003) and authors' surveys (2006–2009) (Appendix S3). To minimize the effects of sampling bias, rate of spread was determined annually as well as for the entire period of range expansion (1997–2009). Longitudinal and areal spread was then plotted against time to estimate minimum rates of spread (as observations of occupancy were made an undetermined length of time after introduction) between 1997 and 2008.

RESULTS

Origin of range expansion

The range expansion of painted reed frogs in the Western Cape Province began during or shortly before the 1998 breeding season (Appendix S3) and originated at or near the western boundary of the Tsitsikamma Forest (National Park headquarters 34°01′18.8″S, 23°53′47.9″E) (Fig. 1).

Of 1308 point localities for the species in the Frog Atlas database dating from 1917 to 2003, only 56 lay to the west of the historical range boundary at Tsitsikamma National Park and all of these were collected after 1997 (Minter *et al.* 2004). Because of their conspicuous call and behaviour, it is unlikely that breeding populations could have remained undetected for more than 1 year prior to this putative introduction in date.

Environmental correlates of occupancy

Eight terms were retained in the minimum adequate spatial model after model simplification (Table 2). The addition of altitude did not result in significantly improved fit, so this variable was removed from the model. All environmental variables except water body area were retained in the minimum adequate environmental model. However, only January evaporative potential (negative relationship), winter degree days (positive relationship) and fringing vegetation around water bodies (positive relationship) contributed significantly (Table 2). Almost two-thirds (64%) of variation in occupancy was explained by the combined model (Table 2; Appendix S4). The spatial variables explained 49% of variation in occupancy and the environmental variables explained 47%.

The combined model contained five significant spatial terms up to the third order (Table 2). Significant environmental variables were fringing vegetation (positive correlation) and January evaporative potential (negative correlation). Floating vegetation and water body density were retained but were not significant (Table 2; Appendix S4).

The maximal model had low variance inflation factors (all VIF <4.4 for linear regression of main effects) and there was no over-dispersion in the maximal or final combined models (residual deviance/residual d.f. = 0.522 in both cases), which justified the default scaling factor of one and confirmed the adequacy of the combined model. Significant positive spatial autocorrelation in occupancy was present in shorter distance classes (classes 1–4, corresponding to 20 grid cells or 100 km). Negative spatial autocorrelation was present in longer distance classes

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Table 2. Minimum adequate spatial and environmental models, and the combined model

Terms retained	Environmental terms dropped from model	Residual deviance	Residual d.f.	Log likelihood	% deviance explained	AIC_c	w_i
Spatial model:							
$x^{\star} + y^{\star} + x^2 + xy^{\star} + y^{2\star} + x^2y^{\star} + xy^2 + y^3$		149.14	202	−74.572	48.77	165.9	<0.001
Environmental model:							
FlVeg + FrVeg* + MAP + JanEvap* + WinterDD* + Wb750m	WbSize	154.16	204	−77.017	47.05	166.6	<0.001
Combined model:							
$y^{\star} + x^{\star} + y^{2\star} + xy^{\star} + xy^{2\star}$ + FrVeg* + FlVeg + JanEvap* + Wb750m	MAP, WinterDD	104.90	201	−52.449	63.97	123.8	0.992

Null deviance for all models = 291.12; null d.f. = 210; statistically significant model terms are identified by asterisks ($P < 0.05$); AIC_c, second-order AIC; w_i, Akaike weight of model in full model set. Abbreviations and units: FlVeg, presence/absence of floating veg.; FrVeg, presence/absence of fringing vegetation at water body; JanEvap, January potential evaporation (mm); MAP, mean annual precipitation (mm); Wb750m, number of water bodies within a 750 m radius; WbSize, water body size (ha); WinterDD, heat units between April and September (degree days; base = 10°C).

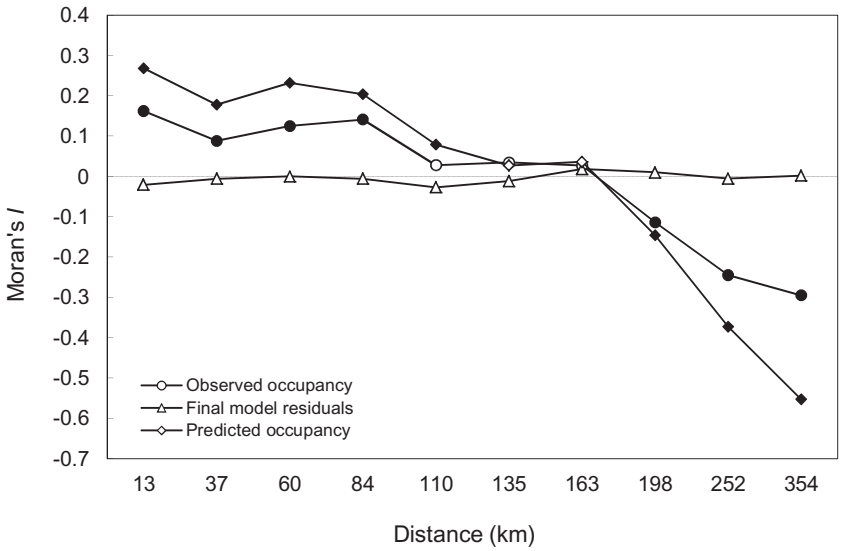

Fig. 2. Spatial autocorrelation structure in the response variable (occupancy), model residuals and predicted values from the combined model. Filled markers represent significant Moran's *I* values, open markers non-significant values; $\alpha = 0.05$; significance tested using 199 permutations; 2194 point pairs per distance class. Correlograms for occupancy and predicted values are significant, while that for model residuals is not significant (Bonferroni correction; $\alpha = 0.05$).

(8–10, corresponding to 40 grid cells or 200 km) (Fig. 2). The residuals of the combined model were not significantly autocorrelated in any distance class, demonstrating that spatial autocorrelation had been removed in the modelling process. No periodicity was evident in the correlograms.

Range structure and extent

The combined dataset of occupancy records from the novel range spanned 12 breeding seasons (1998 to 2009) and contained 151 presence records. The alpha hull (alpha = 2) covered 2869.31 km^2 and could be divided into either two or three discrete populations under alpha = 6 or alpha = 2 respectively (Fig. 1). Both alpha values resulted in a gap in occupancy in the central part of the novel range of 100 km and 140 km, respectively. Occupied sites lay in a narrow latitudinal band between 33°45′48″S and 34°11′45″S, but extended longitudinally from the extreme east (Goukamma Nature Reserve, 22°56′27″E) to the extreme west of the sampling extent (Cape Peninsula, 18°23′11″E).

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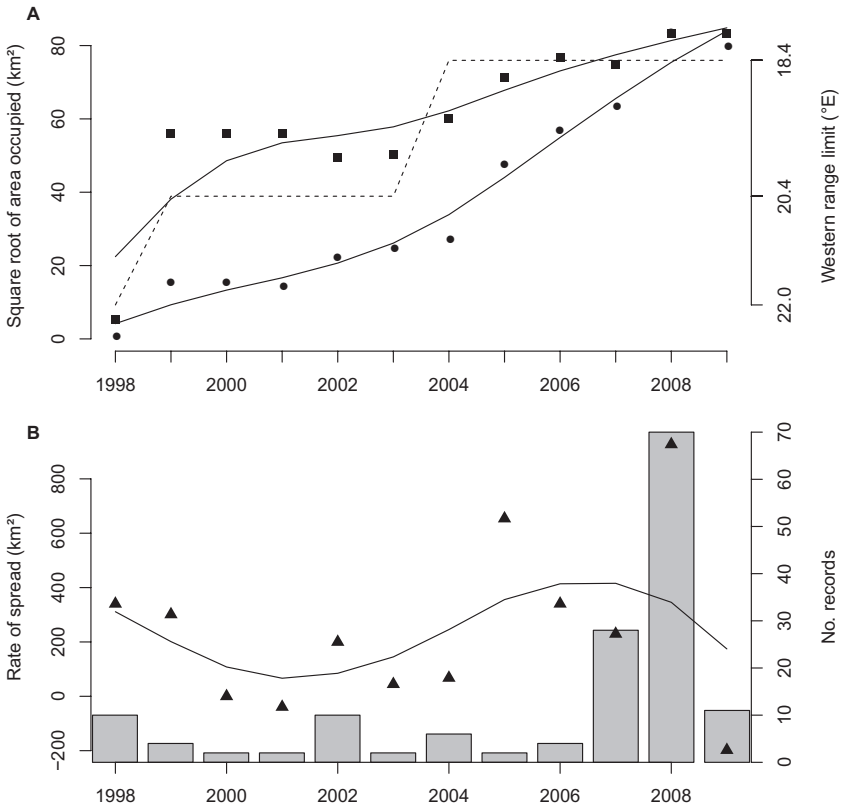

Fig. 3. Temporal trends in *Hyperolius marmoratus* occupancy in the novel range. (A) Minimum area occupied and longitudinal range limit. Area occupied was calculated from annual alpha hulls with alpha = 2 (circles) and alpha = 6 (squares), with curves fitted by cubic spline. Dashed line depicts the cumulative western range limit since start of invasion. (B) Minimum rate of spread and number of presence records used. Rate of spread (triangles) was calculated annually and a cubic spline fitted. Number of records (bars) is the number of presence records in each season. Years refer to the breeding season ending in the specified year.

Rate of spread

Both areal and longitudinal spread rates appeared most rapid in the second part of the study period (2004–2009) but were variable throughout 1998–2009 (Fig. 3). Between 1998 and 1999 the frogs spread westwards from the historical range boundary to the central part of the range (marked 5 on Fig. 1), a distance of 230 km. During this period, the species occupied 22% of its current novel range extent and was restricted to the area east of 20.4°E. Between 2000 and 2003, there was no further increase in western range limit, although the extent of occurrence increased to 30% of the 2009 range extent (Fig. 3; Appendix S5), suggesting that range expansion was followed by filling of unoccupied parts of the range, rather than continuous expansion of the invasion front. In 2004, the frogs were detected around Cape Town in the extreme south-west of the province, demonstrating a further linear range expansion of about 180 km. This range expansion was also followed by local spread (S.J. Davies, unpubl. data, 2009).

DISCUSSION

While the susceptibility of a region to invasion is a combination of organismal, environmental and community characteristics (Richardson & Pyšek 2006), there is strong evidence that anthropogenic disturbance plays a role in facilitating invasion in several important ways. One of these is resource supplementation, as has been demonstrated for Argentine ants (*Linepithema humile*, Menke & Holway 2006) and tropical house geckoes (*Hemidactylus mabouia*, Short & Petren 2011). For pond-breeding amphibians, the presence of additional perennial water bodies in the landscape is even more influential, as it directly affects the availability and quality of breeding habitat (Brainwood & Burgin 2009) and increases landscape connectivity by reducing the average distance between neighbouring water bodies or creating corridors that connect them (Ray *et al.* 2002). Farm dams constitute the majority of water bodies in the Western Cape, and the painted reed frog was found in more artificial than natural water bodies (205 *vs.* 22 water bodies), albeit

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at similar prevalence. Together with the importance of summer aridity (January evaporative potential) in the habitat model this suggests that farm dams have played an important role in the expansion of the species by creating suitable habitat in areas that would not otherwise have provided breeding habitats in summer.

Determinants of invasion and barriers to spread

The identification of January evaporative potential and winter degree days as significant correlates of occupancy in the environmental model confirms our prediction that the presence of painted reed frogs is limited by climatic variables. However, winter degree days did not emerge as a significant variable in the combined model, probably because winter temperatures are closely related to other environmental gradients, such as altitude. Fringing vegetation around water bodies was identified as a significant correlate of occupancy in both the environmental and combined models, confirming our assertion that local habitat quality is an effective predictor of species occupancy at local scales; this is consistent with studies on other anuran species (Brainwood & Burgin 2009).

To further investigate the constraints on range expansion identified by the generalized linear model, we undertook a *post hoc* analysis of environmental conditions at water bodies in the widest gap in the range (between 4 and 5 on Fig. 1) *versus* those within the range boundary. Climate and local habitat quality in the gap appeared to be less hospitable to painted reed frog breeding populations than those within the range boundary (Table 3). For example, water bodies in the gap region had lower mean annual precipitation, higher January evaporative potential, fewer degree days in winter, and lower occurrence of fringing and floating vegetation than those elsewhere in the range, supporting the results of the model.

In contrast, landscape variables such as altitude, water body size and water body density were similar inside and outside the range boundary (Table 3). Part of the gap region is covered by the Riviersonderend mountain range that rises to over 1600 m, so it is likely that rugged terrain and generally higher altitude present barriers to spread. In fact, range edges of multiple animal groups are related to biome boundaries (e.g. Van Rensburg *et al.* 2004 for southern African birds) and areas of habitat and landscape heterogeneity and topographical complexity (McInnes *et al.* 2009 for the Afrotropics). The lack of a clear relationship between altitude and the range boundary in this study may be due to sparser sampling in the mountainous parts of the study area where water bodies are scarce and sometimes inaccessible to sampling. Available data on terrain rugosity (Schulze *et al.* 1997) were highly correlated with climate, and could not be included in the generalized linear model. Nevertheless, the physiological and ecological requirements of amphibians imply that climate variables are likely to play a larger role in range expansion than terrain rugosity at the scale of this investigation.

Table 3. Results of *post hoc* tests of environmental variable values at sites within the range *versus* its largest intervening gap

Variable	Value inside range boundary	Value in gap	Test statistic	
Categorical	Frequency	Frequency	Odds ratio[†]	*P*-value
Occupancy	53/54	1/54	0.018	<0.001
FrVeg[⋆]	106	48	0.317	<0.001
FlVeg[#]	29	8	0.379	0.025
EmVeg	86	47	0.692	0.24
Continuous/discrete	Mean	Mean	W[‡]	
JanEvap[⋆]	285.89	304.1	3124.5	<0.001
WinterDD	755.53	681	7002	<0.001
MAP	522.26	474.95	6537	0.002
Alt	194.96	221.81	4434	0.065
WbSize	2.48	2.82	4645.5	0.177
Wb750m[#]	4.2	3.84	5550.5	0.443

[†]Fisher's exact test. [‡]Wilcoxon rank sum test. Environmental variables retained in the combined model are identified by [#](not significant) and [⋆](significant at $P < 0.05$). $n = 210$ for all tests. Abbreviations and units: Alt, altitude (m a.s.l.); EmVeg, presence/absence of emergent veg.; FlVeg, presence/absence of floating veg.; FrVeg, presence/absence of fringing vegetation at water body; JanEvap, January potential evaporation (mm); MAP, mean annual precipitation (mm); Wb750m, number of water bodies within a 750 m radius; WbSize, water body size (ha); WinterDD, heat units between April and September (degree days; base = 10°C).

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Rate of spread

Spread models of invasive species that assume purely diffusion-based dispersal may underestimate actual rates if at least some dispersal is in fact due to jump dispersal (Skellam 1951; Suarez *et al.* 2001; Short & Petren 2011). Such mixed-mode dispersal, as well as environmental heterogeneity, may produce non-linear spread rates (Shigesada *et al.* 1995; Kot *et al.* 1996; Hui *et al.* 2012). Spatially and temporally heterogeneous spread caused both by diffusion and human-mediated jump dispersal is consistent with the Western Cape's spatially and temporally variable topography, rainfall and rainfall seasonality (Schulze *et al.* 1997; Chase & Meadows 2007). Our results highlight the coupling of different levels of anthropogenic change with long-distance translocation in driving the spread of invasive anurans, further illustrating the importance of spatially and temporally explicit occupancy data for quantifying spread rates and making inferences about dispersal mechanisms.

The most parsimonious explanation of the discrete populations in the novel range is that natural dispersal, or a combination of natural and human-mediated jump dispersal, facilitated spread in the eastern part of the novel range, while human-mediated jump dispersal operated in the west, either from the historical range or from another part of the novel range, across a barrier that could not be breached by natural dispersal, that is, the region associated with the Riviersonderend mountains. The initial rapid increase of area occupied (1998–1999) and the corresponding rapid change in western range limit (Fig. 3A) are likely caused by increased sampling effort at the start of the Frog Atlas project. However, it is possible that diffusion-based spread due to increased habitat availability (artificial water bodies) allowed the frogs to disperse westwards during this period. In contrast, the second significant change in western range limit during 2003 or 2004 strongly suggests an independent long-distance dispersal event across the Riviersonderend mountain range. Rate of spread also became more variable in the later years of the range expansion (Fig. 3B), suggesting that both human-mediated jump dispersal and natural diffusion played their roles in the range expansion.

Dispersal modes and mechanisms

Considerable spatial structure was found in the novel range of the painted reed frog. Retention of second- and third-order terms in the trend surface model shows that there are patches and gaps at the scale of the whole study area (Legendre & Legendre 1998). The relatively large proportion of variation shared by the spatial and environmental models (37%) suggests that the observed spatial patterns are driven by either stochastic events and processes or large-scale geographical gradients. Given the broad longitudinal extent of the sampled area and the east–west trending climatic gradients in the Western Cape (Chase & Meadows 2007), environmental characteristics of sites are likely to be influenced strongly by their position on gradients of rainfall or rainfall seasonality.

The substantial break in continuity in the central part of the range indicates that at least two spatially discrete populations of painted reed frogs exist, separated by a distance of at least 100 km. While there are published (Bishop 2004) and anecdotal reports of adult painted reed frogs being translocated in nursery plants and fresh produce, there is no evidence of natural long-distance dispersal such as transport of eggs on the feet of water birds (see also Measey *et al.* 2007). This pattern suggests human-mediated jump dispersal as the most likely mechanism by which painted reed frogs have occupied the western side of the gap. This view is supported by the finding of Tolley *et al.* (2008) that a single identical mitochondrial haplotype existed in frogs from two dams separated by approximately 40 km of mountainous terrain (marked 2 and 3 on Fig. 1). The identification of one of these sites (3 on Fig. 1) as a spatial outlier of the range in this study implies that human-mediated jump dispersal occurred between these two sites or that propagules were introduced independently to the two dams from the same source. However, the same haplotype is also present in a third dam in the Cape Town area (Tolley *et al.* 2008), making it highly unlikely that three independent introductions of the same haplotype could have occurred. Thus, it is clear from the spread rates and range structure found in this study as well as the identification of barriers to spread, that mixed dispersal modes have contributed to the range expansion of this species. While jump dispersal and diffusion-type spread have operated in the east of the range, jump dispersal alone can account for the rapid expansion to Cape Town in 2003 or early 2004. However, diffusion-based spread is likely to be important at a local scale as jump dispersal cannot account for every introduction to a new water body.

CONCLUSION

By including the entire spatial and temporal extent of the recent and ongoing range expansion of the painted reed frog in the Western Cape, we have shown that the species has expanded its range rapidly over little more

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than a decade to occupy largely artificial habitats across the novel range. However, its distribution in the novel range is limited by summer aridity and winter low temperatures, and associated with the presence of fringing vegetation around water bodies. This extra-limital range expansion shows that a combination of human-mediated jump dispersal and landscape changes, such as the construction of artificial water bodies, allows invasive amphibians to overcome their historical range limits and barriers to spread. It is likely that spread by natural diffusion and human-mediated events will continue in the Western Cape within the bounds of the climatic and local habitat quality requirements of the species.

In the novel range the painted reed frog appears to fill the role of 'urban exploiter' (Kark *et al*. 2007), being almost restricted to farm dams and ponds in highly modified agricultural and urban areas. It meets several of the criteria for urban exploiter status outlined by Kark *et al*. (2007), having an unspecialized diet, gregarious habits at least during the breeding season, a lack of migratory behaviour and considerable behavioural flexibility. From a conservation perspective, the unspecialized requirements, rapid spread and high local population numbers of the painted reed frog suggest that it may compete with native species, in particular the fynbos endemic arum lily frog. Given that the painted reed frog is currently present in one out of every four dams, the novel range is not saturated, and there is still room for expansion within the network of artificial water bodies available.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods for trend surface analysis.
Appendix S2. Descriptive statistics of variables used to explain occupancy.
Appendix S3. Summary of point location records.
Appendix S4. Coefficients of terms retained in the minimum adequate models.
Appendix S5. Details of range expansion.

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